

**Monograph of the Spathidiida  
(Ciliophora, Haptoria)**

**Vol. I: ProtoSPATHIDIIDAE, ARCUSPATHIDIIDAE,  
APERTOSPATHIDIIDAE**

Wilhelm Folsomer and Kuidong Xu

The spathidiids belong to the ciliate subclass Haptoria (Protista, Ciliophora), that is, they are predators using ciliates to overcome the prey. Spathidiid ciliates prefer terrestrial and subterrrestrial habitats, but many occur also in freshwater and some are marine.

Over 200 nominal spathidiid species have been described, sometimes based on seemingly minute differences. Thus, many protozoologists considered them as indeterminate and claimed for a debated revision. The present monograph carefully reviews the taxonomy, nomenclature, and ecology of all nominal species and shows that spathidiid diversity has been greatly underestimated. Based on the re-investigation of described species with modern methods (phase-contrast, scanning electron microscopy) and the first description of over 50 new species, the family Spathidiidae is split into four families and 46 genera. Each species is described and figured in detail, making it unnecessary to go back to the original literature often difficult to obtain. Two identification keys are provided, viz., one for taxonomy and another, single key for users not specifically trained in ciliate taxonomy.

This first part of the monograph contains the families ProtoSPATHIDIIDAE, ARCUSPATHIDIIDAE, and APERTOSPATHIDIIDAE. The second part will contain the family Spathidiidae and a new family, the Pharyngospathidiidae. This monograph is part of our attempt to revise the free living ciliates.



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 **Springer**

MONOGRAPH OF THE SPATHIDIIDA (CILIOPHORA, HAPTORIA)

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# Monograph of the Spathidiida (Ciliophora, Haptoria)

Vol I: Protospathidiidae, Arcuospathidiidae,  
Apertospathulidae

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## Preface

This book continues our series of ciliate monographs, several of which have been published or are in preparation: class Colpodea (FOISSNER 1993); suborder Hypotrichia (BERGER 1999, 2005; volume 3 in preparation); and order Oligotrichida (AGATHA, in preparation). Furthermore, there are several thematic monographs available, viz., on the ciliates used as bioindicators in water quality assessment (FOISSNER et al. 1991, 1992, 1994, 1995); on the ecology and taxonomy of limnetic plankton ciliates (FOISSNER et al. 1999); on soil ciliates from Namibia (FOISSNER et al. 2002); and on the generic names of the ciliates (AESCHT 2001). Altogether, we described and revised over 1000 ciliate species in these monographs, that is, circa one tenth of the species described, but only one thirtieth of the diversity proposed (FOISSNER 1999b, c, 2004a). Certainly, this is far from being complete, but our detailed revisions will be long-lived, and we are optimistic to do some further monographs, even in a time where molecular biology overwhelms most other biological disciplines.

The family Spathidiidae belongs to the subclass Haptoria, a group of rapacious, "lower" holotrichs. The family comprises about 200 described species, most belonging to the time-honoured genus *Spathidium*. Several colleagues doubted the validity of so many *Spathidium* species (BUTKAMP 1977b, FINLAY et al. 1996, WENZEL 1955). However, our monograph shows not only the validity of most described species, but adds 50 new species discovered in over 500 samples from terrestrial biotopes worldwide. Thus, the spathidiids are as diverse as proposed by KAHL (1930a, b) 75 years ago! Now, they consist of over 250 species distributed in four families and 20 (!) genera, several of which will be described in this monograph or were established rather recently. About half of the species have been described or redescribed with modern methods, and thus each needs an average of eight printed pages in the revision. Accordingly, the over 200 species will be not squeezed into a single, large volume with 1000 pages, but they are split into two parts which form a harmonic unit, but can be used also independently. Further, the split facilitates publication, which was considerably delayed because we had to perform basic investigations on ontogenesis, conjugation and resting cysts as well as to describe nearly 100 populations half of which represented new species.

Our monograph is also a first attempt to standardize ciliate species descriptions by fixing and/or quantifying as many features as possible, for instance, the shapes of body and extrusomes, distances, and other "abouts". Indeed, most ciliate descriptions are imprecise using, for instance, different names for the same shape. Botanists recognized the resulting problems very early and thus established descriptive baselines many years ago (STEARNS 1992).

We earnestly hope that our revision will be of use for a long time, not only to taxonomists, but also to ecologists and molecular biologists who not yet recognized the bioindicative capacity of protozoa (FOISSNER 1987a, 1997b) and the many interesting species this group contains.

Salzburg, August 2005

Wilhelm Foissner  
Kuidong Xu

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The thousands of figures comprising the plates are either originals or reproductions from widely scattered sources in the vast protozoological literature of the past 150 years. Specific acknowledgements are generally made in the explanations to the figures: there are named the authors of the papers in which the illustrations originally appeared. Likewise, those colleagues who provided samples, often from remote and/or special habitats, are acknowledged in the individual species descriptions.

Last but not least, we wish to acknowledge the indispensable financial aid from the Austrian Science Foundation (FWF) which, after the recommendation of peer-reviewers, granted the project with a research assistant (Dr. Kuidong XU) and a part-time technician.



## A General Section

As explained in the preface, the monograph has been split into two volumes. This applies also to the general section. In volume I, the general morphology, the life cycle, and the principal investigation methods are described, while volume II will deal mainly with ecology and geographic distribution, phylogeny, evolution, and classification. Further, it will contain a user-friendly key to all species.

### 1 Morphology and Principal Terms

In this section, the principal morphology and terminology will be explained, using simple but well-defined figures. Indeed, this is a first step to the urgently needed general methodology of ciliate descriptions. Partly, figures and terms were taken from STEARN (1992), who reviewed the terms used in descriptive botany. There are still some uncertainties, also in botanical terminology, which should be clarified in a more comprehensive treatment of the matter.

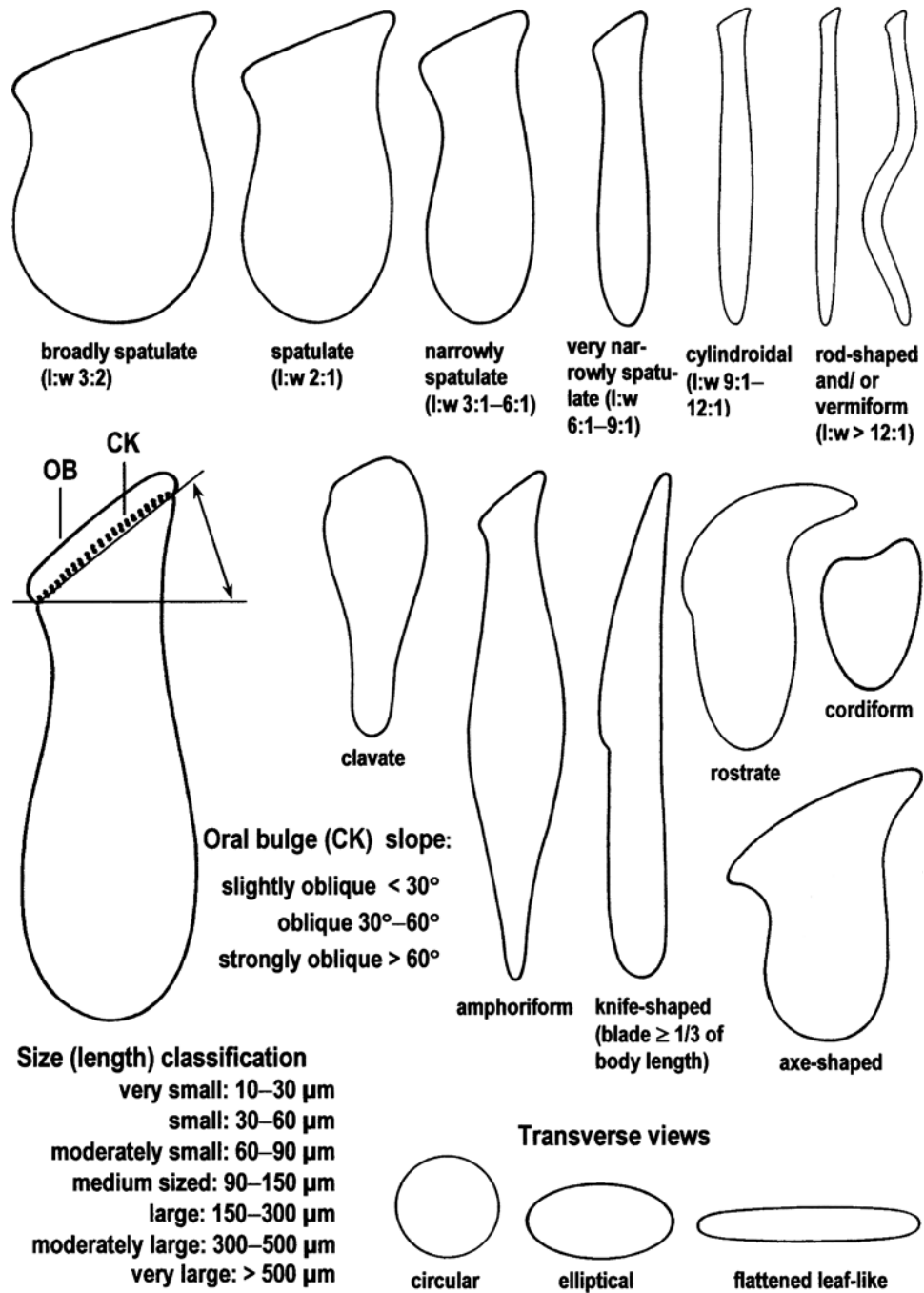
For general ciliate terminology, we refer to the excellent compilations of CORLISS (1979) and MARGULIS et al. (1993), while the general ciliate morphology is exhaustively treated in CORLISS (1979) and PUYTORAC (1994).

#### 1.1 Size and shape, morphometry (Fig. 1–3, 5)

The spathidiids range from about  $60 \times 10 \mu\text{m}$  to  $400 \times 50 \mu\text{m}$  in vivo. The volume of one of the largest species, that is, *Epispathidium securiforme* is 35 times larger than that of one of the smallest species, that is, *Edaphospathula minor*. This is a small range when compared to those found in colpodids (200 000, FOISSNER 1993) and oxytrichid stichotrichs (140, BERGER 1999). We have used seven categories of size (as reflected in body length; arbitrarily if unrealistically set up with non-overlapping ranges) as follows: very small, 10–30  $\mu\text{m}$ ; small, 30–60  $\mu\text{m}$ ; moderately small, 60–90  $\mu\text{m}$ ; medium sized, 90–150  $\mu\text{m}$ ; large, 150–300  $\mu\text{m}$ ; moderately large, 300–500  $\mu\text{m}$ ; very large, > 500  $\mu\text{m}$ .

According to the name, spathidiids should be spatula-shaped. Unfortunately, this hardly applies (Fig. 1–3, 5)! Most are very narrowly to broadly bursiform with a more or less slanted anterior end and a rounded posterior. Others are cylindroidal, vermiform, clavate, axe-shaped etc. Thus, a huge variety of shapes exists, and the ratio of body length to body width ranges from about 1:1 to 30:1. Most species are slightly to distinctly flattened laterally, some are even leaf-like. Many of the terrestrial species are small and/or slender, as is typical for soil organisms in general (FOISSNER 1987a). However, those living in mosses and leaf litter may be large, for instance, the common *Epispathidium amphoriforme*. The shape is stabilized by bundles of cortical microtubules (WILLIAMS et al. 1981), but usually the cortex remains flexible and the shape may thus strongly deform in over- or under-nourished cells. Theronts and trophonts occur, but true polymorphism is lacking. Likewise, metaboly and pronounced contractility do not occur because myonemes are absent.

Invariably, the oral apparatus occupies the anterior body end, forming a more or less



**Fig. 1** Classification (terminology) of body shape in lateral and transverse view, size (length), and slope of oral bulge in spathidiid ciliates. CK – circumoral kinety, l:w – ratio of body length to width, OB – oral bulge.

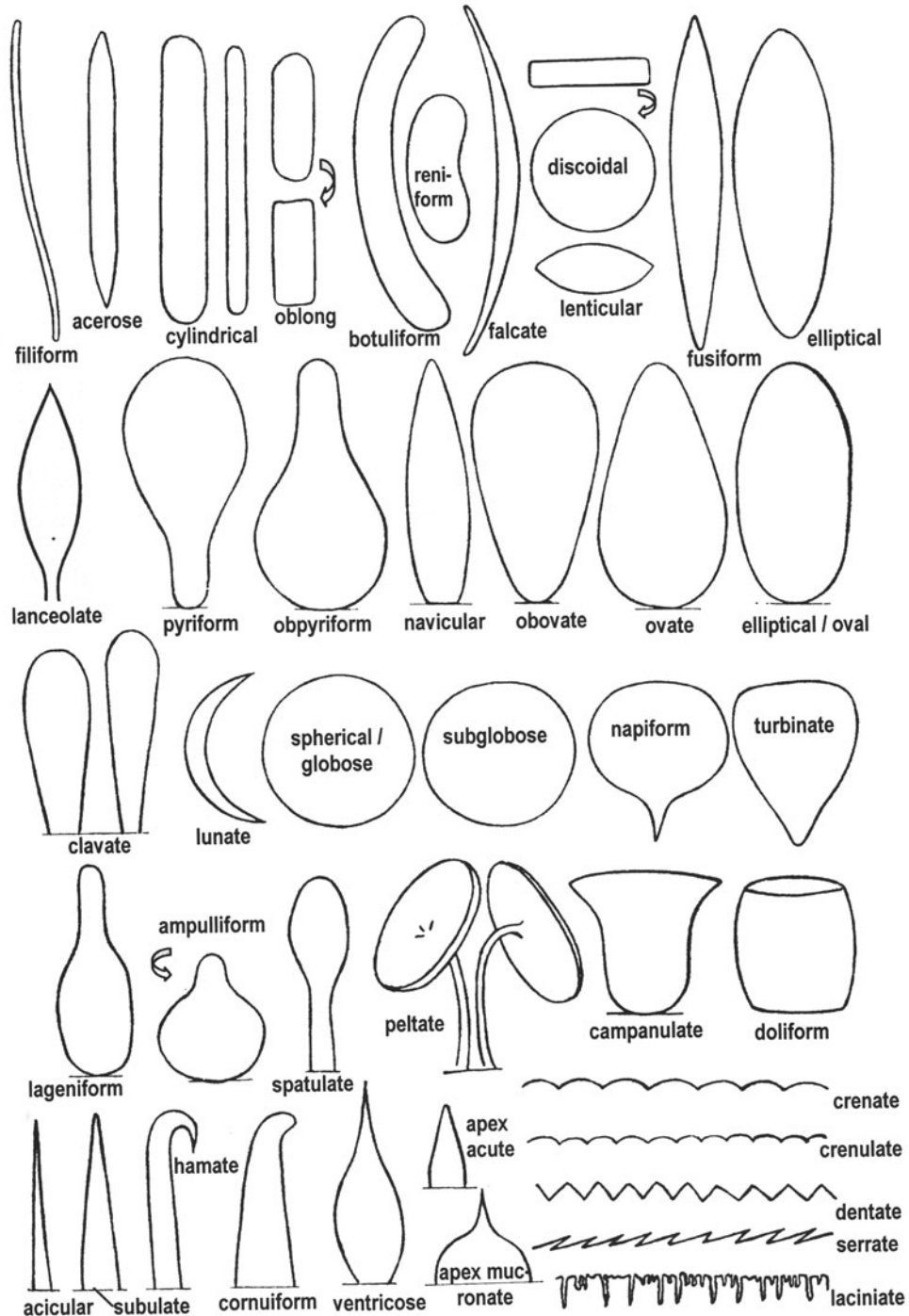


Fig. 2 Terminology of shapes/outlines. From STEARN (1992), modified.



distinct bulge rarely extending to posterior body end (genus *Rhinothrix*). The bulge, respectively, the anterior body end is more or less slanted. Thus, bulge length is a composite of body width and bulge slope. We have used three categories of bulge slope as follows: slightly oblique,  $< 30^\circ$ ; (ordinarily) oblique,  $30\text{--}60^\circ$ ; strongly oblique,  $> 60^\circ$  (Fig. 1).

Detailed morphometrics are available from about 150 populations belonging to circa 100 species, mainly due to the investigations of FOISSNER (1984), FOISSNER et al. (2002), and the present monograph. These data show that the mean coefficients of variation are very similar to those found in colpodids, stichotrichine hypotrichs, and other kinetofragminophoran ciliates (BERGER 1999, FOISSNER 1984, 1993, FOISSNER et al. 2002). Accordingly and in the contrast to the widespread assumption (e.g., WENZEL 1955), spathidiids are as variable or stable as other ciliate groups. The impression of a special variability of the spathidiids is caused by observations of a few species in pure cultures, where variability is indeed high – not only in spathidiids but also in most other ciliates. Malformed specimens can survive and sometimes even reproduce in pure cultures due to the optimal food supply, while they usually die in nature. The number of ciliary rows usually varies only slightly, that is, between 5–10% and is thus one of the most important features for species recognition. Most other characteristics vary between 10% and 20%, while body length:width ratio and the number of macronucleus nodules in multinucleate species have high coefficients of variation between 20 and 40%. The morphometric data give important information about the stability of features and their significance for species recognition. Thus, all descriptions should be accompanied by morphometrics of at least the main features.

## 1.2 Nuclear apparatus (Fig. 4)

Spathidiids have a single macronucleus and micronucleus or many macronucleus nodules and several micronuclei. The shape of the macronucleus ranges from globular to a long, tortuous strand, which may be band-like flattened, a curious feature described only recently (FOISSNER et al. 2002). The micronuclei may be globular, ellipsoidal, lenticular, narrowly ovate, or bluntly fusiform. Altogether, we have distinguished 16 macronuclear and 10 micronuclear configurations (Fig. 4). This high diversity makes the nuclear apparatus to one of the most important features for species recognition. The patterns are as stable or as variable as those of other ciliates and are sometimes obscured by post-divisional, post-conjugational, or ontogenetic reorganization processes (MOORE 1924a, b, XU & FOISSNER 2004). **When in doubt, look at very early dividers which invariably show the “real” nucleus pattern.** So far, chromatin extrusion has not been described.

The macronucleus contains globular, oblong, or irregular dense masses about 1–5  $\mu\text{m}$  in size. Usually, they are recognizable in vivo and impregnate deeply with protargol. There is some indication that these inclusions represent nucleoli: (i) the central mass of the macronucleus of *Colpoda steinii* and *Dileptus* sp. deeply impregnates with protargol and represents a compound nucleolus, according to cytochemical and electronmicroscopical investigations (FOISSNER 1993, RAIKOV 1982); (ii) chromatin bodies are usually smaller than 1  $\mu\text{m}$  and numerous, while nucleoli are often larger than 1  $\mu\text{m}$  and comparatively rare (RAIKOV 1982). These two features apply to the macronuclear structures impregnating with various protargol methods. Thus, we designate these

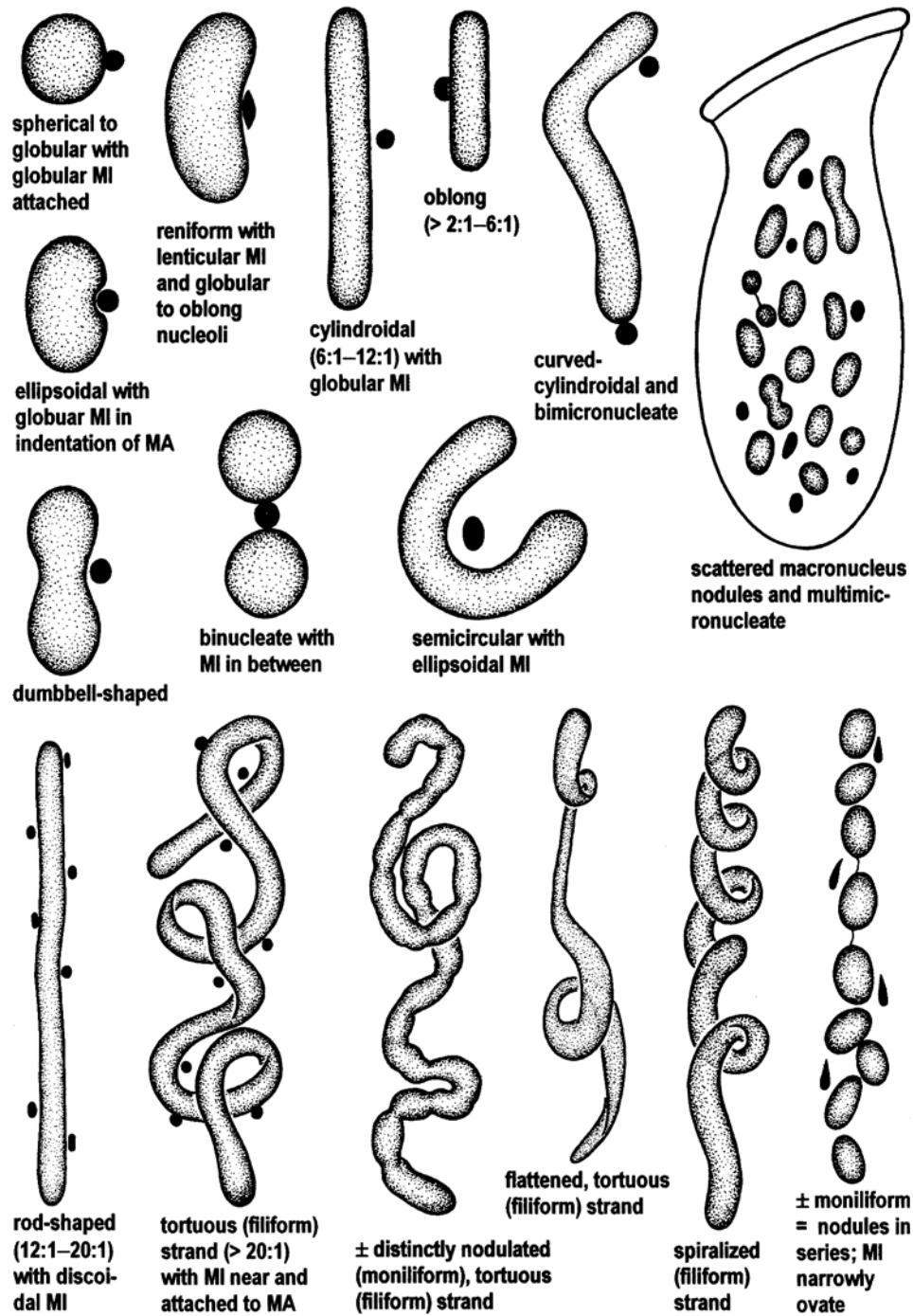


Fig. 4 Shapes of macronucleus and micronucleus in spathidiid ciliates. Nucleoli shown only in the reniform type. MA – macronucleus, MI – micronucleus.

structures as "nucleoli", being aware that this needs confirmation by cytochemical investigations. See BOHATIER et al. (1978) for a brief electronmicroscopical description of the nuclear apparatus of *Epispathidium amphoriforme*.

### 1.3 Contractile vacuole and cytopye (Fig. 5)

Most spathidiids have a single contractile vacuole in posterior body end; few have a second contractile vacuole with distinct excretory pores underneath the dorsal brush, that is, above mid-body, for instance *Arcuospathidium bulli*; and some have several contractile vacuoles, each with their own excretory pores, in a dorsal and/or ventral row (Fig. 5). The bivacuolate pattern evolved independently in *Spathidium* and *Arcuospathidium*, while the multivacuolate pattern is diagnostic of the genus *Supraspathidium* (FOISSNER 2003c). Usually, the vacuole is a simple blister surrounded by smaller collecting vesicles during the diastole. Some species of doubtful classification have a more or less conspicuous collecting canal which supplies the main vacuole, for instance, *Spathidium latissimum* and *Supraspathidium teres* (Vol. II).

The fluid collected by the contractile vacuole is expelled via one or several ordinary excretory pores. Usually, the pores are scattered in the posterior pole area, sometimes they are slightly subterminal on the ventral or dorsal side, and in a few tailed species they are far subterminal, for instance, in *Spathidium apospathidiforme* and *Apospathidium atypicum* (Vol. II).

The cytopye is known in only few species, where it is in the posterior area, that is, near the excretory pores of the contractile vacuole. In some species, for instance, *Rhinothrix porculus*, the fecal mass traverses the contractile vacuole when it is expelled.

### 1.4 Extrusomes (Fig. 5–7)

Shape, size, and arrangement of the extrusomes are highly diverse and are thus a main diagnostic feature of the individual species (Fig. 5–7). This was already emphasized by KAHL (1930a, b). Accordingly, the extrusomes must be carefully studied in vivo because they often become distorted in silver preparations or do not impregnate at all. Indeed, the extrusome features are so important that species cannot be recognized without this information.

Most or even all spathidiids are predators. Thus, they have toxicysts, except of some curious species which lack toxicysts at all. About one third of the species has two shape and/or size types of toxicysts, and some even have three kinds, for instance, *Rhinothrix porculus*. Further, (likely) all spathidiids have at least one kind of mucocysts, appearing as "cortical granules" (Fig. 7).

The toxicysts are studded in the oral bulge and scattered in the cytoplasm; additionally, they may be attached to the somatic cortex. For determining the shape, size, and arrangement of the toxicysts only fully developed (mature) toxicysts may be used, that is, those which are anchored to the oral bulge or somatic cortex (Fig. 5, 6); cytoplasmic toxicysts are frequently not fully developed. This is evident, inter alia, from their impregnation capacity: anchored toxicysts usually do not impregnate with protargol, while various cytoplasmic developmental stages often impregnate rather deeply.

Shape and arrangement of the mucocysts are much less diverse, at least in the light